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ScienceDirect
Forest Ecology and Management 240 (2007) 87–95
Forest Ecology and Management
www.elsevier.com/locate/foreco

Coarse woody debris and canopy cover in an old-growth Jeffrey pine-mixed conifer forest from the Sierra San Pedro Martir, Mexico

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Received 5 August 2006; received in revised form 12 December 2006; accepted 12 December 2006

Abstract

The cultural practices associated with Euro-American settlement in the United States have altered forest structure and ultimately changed fundamental ecosystem processes. Coarse woody debris (CWD) and canopy cover are recognized as having great importance for many wildlife species and ecological processes. Little information is available from forests on historical levels of canopy cover and CWD before European settlement. A great deal of uncertainty exists concerning the long-term role of fire and the dynamics of CWD, especially in forests that once experienced frequent, low-moderate intensity fire regimes. The objective of this study was to quantify CWD and forest canopy cover in an area where harvesting has never occurred and limited fire suppression began in the 1970s. This study was done in Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir (SSPM) in northwestern Mexico. Canopy cover, canopy closure, and CWD were sampled on a grid of plots. Average canopy cover was 26.8%, average canopy closure was 40.1%. A total of 102 CWD pieces were measured, and nearly half of the plots (45.7%) had no CWD present. Average CWD density, percent cover, volume, and weight were 108 pieces ha^{-1}, 1.5%, 47.5 m^3 ha^{-1}, and 15.7 tonnes ha^{-1}, respectively. All of the CWD sampled were in the later stages of decay. Less than average values for CWD density, percent cover, volume, and weight were recorded in 57%, 64%, 67%, and 69% of the plots, respectively. CWD dynamics in forests that experience frequent, low-moderate intensity fires are fundamentally different than those having long-interval, high-severity fires. There was a large amount of variability in all CWD and forest canopy cover measurements taken from Jeffrey pine-mixed conifer forests in the SSPM. Spatial heterogeneity in forest structure should be included in the desired conditions of xeric, pine-dominated forests in the United States that once experienced frequent, low-moderate intensity fire regimes. It should be noted that heterogeneity by itself may not lead to sustainable forests unless that heterogeneity includes stand structures that are resistant/resilient to high-severity fire, drought, insects, and disease.

Keywords: Baja California; Coarse downed wood; Desired conditions; Canopy closure; Crown closure; Peninsular range; Ponderosa pine; Habitat

1. Introduction

The cultural practices associated with Euro-American settlement in the western United States (i.e. large-scale logging, livestock grazing, and fire suppression) have altered forest structure and ultimately changed fundamental ecosystem processes (Minnich et al., 1995; Fulé et al., 2002; Skinner, 2002; Knapp et al., 2005). A common goal in forest management in the western United States (US) is to increase resistance in forests such that natural ecosystem processes can predominate. Often the density and size distribution of trees in a forest stand are the primary interest in defining management targets. However, the aerial structure of forest stands, as well as the structure of the forest floor, are also important.

Coarse woody debris (CWD-wood on the forest floor that is not incorporated into the humus or mineral soil (Muller and Liu, 1991)) is recognized as having great importance for many wildlife species and ecological processes (Harmon et al., 1986; Spies et al., 1988; Apigian et al., 2006). Similarly, canopy cover influences resource availability on the forest floor and also

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doi:10.1016/j.foreco.2006.12.012

affects wildlife habitat. Despite the importance of these forest structural characteristics, little information is available in the US on levels of canopy cover and CWD prior to European settlement (Skinner, 2002).

The role of dead wood in an ecosystem depends largely on such characteristics as size and form, orientation, and resident flora and fauna (Steed and Wagner, 2002). The first CWD studies in North America came from subalpine balsam fir (*Abies balsamea* (L.) P. Mill.) forests (Lambert et al., 1980), Rocky Mountain lodgepole pine (*Pinus contorta* spp. *latifolia* Dougl.) forests (Romme, 1982; Fahey, 1983), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests in western Oregon and Washington (Spies et al., 1988). All of these forests experience high-severity, stand-replacement fires with relatively long-intervals between fires (100–400 years). In these ecosystems, CWD is recruited episodically coincident with high-severity fire and to a lesser degree, during stand development.

The majority of CWD studies in western North America have been done in old forests that have experienced approximately a century of fire suppression with or without partial harvesting (Ohmann and Waddell, 2002; Skinner, 2002). As a result, a great deal of uncertainty exists concerning the long-term role of fire and the dynamics of CWD, especially in forests that once experienced frequent, low-moderate intensity fire regimes. As Robertson and Bower (1999) write ‘Unknown, unfortunately, are typical loadings of CWD in presettlement forests.’ This paper addresses the issue poised by Robertson and Bower (1999).

Forest canopy cover is an important structural component of forest ecosystems. Many wildlife species select stands with differing amounts of cover, others are found over broader levels of canopy. Common measures of the forest canopy include canopy cover and canopy closure (Jennings et al., 1999). Canopy cover is the proportion of the forest floor covered by the vertical projection of the tree crowns; canopy closure is the proportion of a segment of the sky hemisphere obscured by tree crowns from a single point (Jennings et al., 1999).

One large forested ecosystem exists in northwestern Mexico where harvesting has been rare and a policy of large-scale fire suppression was never initiated, the Sierra San Pedro Martir (SSPM), Baja California, Mexico (Minnich et al., 1997; Stephens et al., 2003; Stephens and Fulé, 2005). This area is composed of coniferous forests and shrublands of the Californian floristic province that occur nowhere else in Mexico (Minnich et al., 1997; Minnich and Franco-Vizcaíno, 1998; Minnich et al., 2000).

The SSPM is unique within the California floristic province in that its forests are influenced by lightning ignited fires similar to those that could occur in many pine-dominated forests in the western US. Median composite fire return intervals in Jeffrey pine (*Pinus jeffreyi* Grev. and Balf)-mixed conifer forests in the SSPM from 1700 to 2000 varied from 7 to 15 years (Stephens et al., 2003), and this is comparable to past fire frequency in similar forests in California (Skinner and Chang, 1996; Stephens, 2001; Taylor, 2004). Limited fire suppression began in the SSPM in the mid 1970s but this has mostly consisted of one or two four-person hand crews in the summer and fall periods.

The SSPM has experienced livestock grazing at varying intensities over the last 200 years (Minnich et al., 1997; Minnich and Franco-Vizcaíno, 1998). A recent study quantified the concentration of grass phytoliths in the understory of Jeffrey pine-mixed conifer forests and found values consistent with the interpretation of a forest lacking a grass understory (Evett et al., in press). This provides important evidence that the introduction of livestock did not remove an understory with a high amount of grasses as found in the southwestern US (Fulé et al., 2002).

The objective of this study was to develop information on the density, percent cover, volume, weight, and age of CWD in a western North American coniferous forest that has not been impacted by fire suppression or harvesting. This study also quantified canopy cover and canopy closure of this forested ecosystem because they are also important structural characteristics. This information is then compared to coniferous forests in the US with different land-use histories. Information from this study can assist in the development of desired future conditions in similar forests in the western US and may be of interest to ecologists modeling the dynamics of mixed-conifer forests.

2. Methods

2.1. Study location

The study was conducted in the SSPM National Park (31°37′ N, 115°59′ W) located approximately 120 km SE of Ensenada, Mexico. The SSPM is the southern terminus of the Peninsular Mountain Range that begins at the boundary between the San Jacinto and San Bernardino Mountains in California; approximately 350 km separates the SSPM from the San Bernardino Mountains. The fauna and flora of the SSPM is very similar to that found in the US portion of the Peninsular Range.

Forests in the SSPM are composed of Jeffrey pine, white fir (*Abies concolor* [Gord. and Glend.] Lindl), sugar pine (*Pinus lambertiana* Dougl.), lodgepole pine (*P. contorta* var. *murrayana* Dougl. ex. Loud.), and limited amounts of incense-cedar (*Calocedrus decurrens* [Torr.] Floren.) and quaking aspen (*Populus tremuloides* Mich). The most common forest types are Jeffrey pine, Jeffrey pine-mixed conifer, and mixed white fir forests, respectively (Minnich and Franco-Vizcaíno, 1998). Floristically, forests in the SSPM are very similar to portions of the eastern Sierra Nevada and southern California mountains (Minnich et al., 1995; Stephens, 2001; Taylor, 2004; Stephens and Fry, 2005; Stephens and Gill, 2005).

The soils of the SSPM are unclassified but those in the study area are Entisols (Stephens and Gill, 2005). Soils are shallow, well to excessively drained, and relatively acidic. The most common soil texture is loamy sand; parent material is diorite. Similar forest soils have been classified as Typic Xeropsamments by Franco-Vizcaíno et al. (2002); soil chemical properties in SSPM meadows were also very similar to SSPM and San Jacinto forests (Sosa-Ramírez and Franco-Vizcaíno, 2001;

Franco-Vizcaíno et al., 1992). Soil chemistry and texture from the study area are typical of granite-derived soils in similar forests in the eastern Sierra Nevada in California (Potter, 1998).

The SSPM is located in the southern margin of the North American Mediterranean climate zone (Pyke, 1972; Markham, 1972; Minnich et al., 2000); however, weather data from this area are limited because there is no permanent weather station in this range. Average annual precipitation collected by a set of temporary weather stations in the upper plateau (Vallecitos Meadow) from 1989 to 1992 was 55 cm (Minnich et al., 2000). The Mediterranean climate in the SSPM possibly includes higher amounts of summer precipitation than most areas of California (Stephens et al., 2003) but this requires further study because of the limited precipitation record.

Forest structure has been inventoried in Jeffrey pine-mixed conifer forests in the SSPM using a 200 m × 200 m systematic grid of plots from an area of approximately 144 ha (Stephens, 2004; Stephens and Fry, 2005; Stephens and Gill, 2005). In this area, average tree DBH was 32.6 cm (range 2.5–112 cm), average tree density was 145.3 trees ha^{-1} (range 30–320 trees ha^{-1}), average basal area is 19.9 m^2 ha^{-1} (range 5.7–50.7 m^2 ha^{-1}), and average snag density in 2003 was 5.10 snags ha^{-1} (range 0–25 snags ha^{-1}). Regeneration patch fraction was 3.8% and patch abundance was 8.5 ha^{-1}. Average surface fuel loads were 15.8 tonnes ha^{-1} (range 0.01–159.74 tonnes ha^{-1}) in the study area.

2.2. Field measurements

Canopy cover and canopy closure were sampled on a grid of 121 plots and CWD was sampled on 81 plots that were installed within a portion of the 144 ha area described above; the placement of this portion was chosen randomly. Mexican topographic maps were used to select the 144 ha area with uniform aspects (west, northwest), slopes (0–20%), and soil parent material (diorite) to reduce variability in forest structure that could be caused by these abiotic factors. Elevation in the sampled area varied between 2500 and 2600 m and it is approximately 1.2 km west of the northern portion of Vallecitos Meadow in the SSPM National Park. Previous research has shown the high degree of spatial variability in SSPM forests (Stephens, 2004; Stephens and Gill, 2005) suggesting spatial dependence is unlikely and individual plots can be assumed to be independent samples.

Plots were separated by either 25 or 50 m and the study area covered approximately 16 ha (Fig. 1). Estimates of percent canopy cover and canopy closure were measured using two instruments; a concave mirror densiometer and a sight tube. Densiometer measurements were taken at the plot center by tallying the number of points under canopy, facing each of the four cardinal directions. For the sight tube, a 5 × 5 grid was overlain at each plot at 5 m spacing. At each point on the grid, the sight tube was used to determine if a tree crown was directly overhead; the species of the tree was recorded if the grid point was under canopy. Percent canopy cover was estimated by the total number of points under canopy divided by the total number of grid points sampled (25).

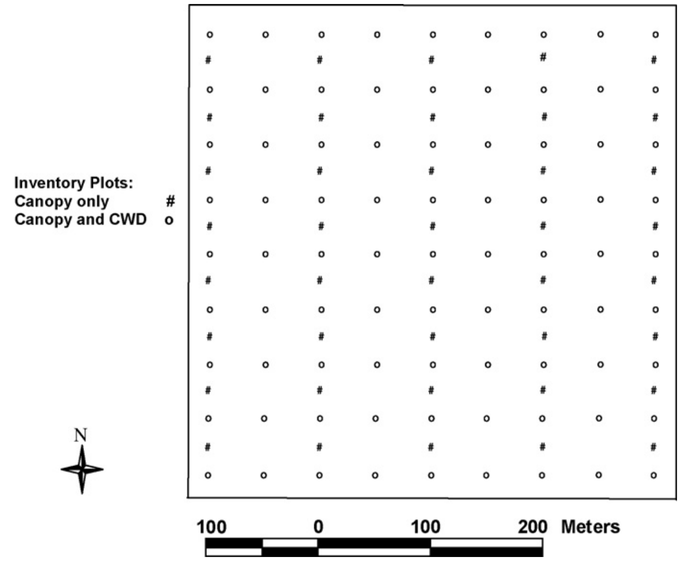

Fig. 1. CWD and canopy cover/closure sampling design in an old-growth Jeffery pine-mixed conifer forest in the Sierra San Pedro Martir, Mexico.

For CWD, a random azimuth was chosen at each plot and all qualifying CWD, logs greater than 1 m in length and with a large end diameter at least 15 cm, were measured within a 4 m × 20 m belt transect (Bate et al., 2004). For each qualifying log, the following attributes were recorded: species, small and large end diameters, total length, length within transect, and whether or not the mid-point of the log fell within the transect. The decay class of each log was given a classification of 1–5 as described by Waddell (2002). For the study area, characteristics of CWD (density ha^{-1}, percent cover ha^{-1}, volume (m^3 ha^{-1}), and weight (metric tonnes ha^{-1})) were computed using equations described by Bate et al. (2004).

At each plot a chainsaw was used to cut wedges from 1 to 2 pieces of CWD in order to determine the date that individual tree died; the piece selected for sampling was chosen randomly. Each wedge contained at least 100 annual rings and was sanded so that tree rings could be readily distinguished under a microscope. The year of tree death can be determined by crossdating tree rings in the wedges using standard dendrochronological techniques (Stokes and Smiley, 1977; Swetnam et al., 1985). Previous work that quantified the fire history in the SSPM (Stephens et al., 2003) did so by visually comparing wedge tree-ring series with a nearby chronology (Stokes et al., 1971) obtained from the International Tree-ring Data Bank (Grissino-Mayer and Fritts, 1998). It was hoped that a dendrochronological analysis of CWD would help elucidate the dynamics and longevity of CWD (Robertson and Bower, 1999).

3. Results

3.1. Canopy cover and closure

Average canopy cover was 26.8% and canopy closure was 40.1% using the sight tube and spherical densiometer, respectively. On average, canopy cover estimates were 13.4% lower than estimates of canopy closure (Table 1). For

Table 1
Tree canopy cover (sight tube) and closure (densiometer) in Jeffrey pine-mixed conifer forests in the SSPM ($n = 121$)

	Densiometer (%)	Sight tube (%)	Sight tube (%) by species			
			JP	WF	SP	LP
Average (S.E.)	40.1 (1.6)	26.8 (1.1)	20.6 (1.1)	4.3 (0.5)	1.3 (0.3)	0.4 (0.2)
Median	39.5	26.0	20.0	0	0	0
Minimum/maximum	0/87.6	0/56.0	0/52.0	0/24.0	0/16.0	0/8.0

JP, Jeffery pine; WF, white fir; SP, sugar pine; LP, lodgepole pine. S.E. is the standard error of the mean.

Table 2
CWD characteristics in Jeffrey pine-mixed conifer forests in the SSPM ($n = 81$)

	Diameter (cm)	Decay class	Density (pieces ha^{-1})	% Cover (ha^{-1})	Volume (m^3 ha^{-1})	Weight (tonnes ha^{-1})
Average (S.E.)	33.5 (1.6)	3.8 (0.8)	108.1 (16.3)	1.5 (0.2)	47.5 (9.3)	15.7 (3.2)
Median	30.0	4.0	0	0.4	5.0	1.4
Minimum/maximum	14/96	2/5	0/625.0	0/8.4	0/386.6	0/154.4

S.E. is the standard error of the mean.

80.8% of the plots, canopy cover was lower than canopy closure. Both measures exhibited approximately normal frequency distributions (data not shown).

Jeffrey pine accounted for 76.9% of the average canopy cover using the sight tube (Table 1). Canopy cover was substantially lower for white fir (16.0%), sugar pine (4.9%), and lodgepole pine (1.5%). For 40.1% of the plots, Jeffery pine accounted for all of the canopy cover. Canopy cover was highly variable within the sampled forest (Fig. 2).

3.2. Coarse woody debris

A total of 102 CWD pieces were measured in 44 of 81 plots. Nearly half of the plots (45.7%) had no CWD present (at least 1 m in length and with a large end diameter at least 15 cm). Average CWD load was 15.7 metric tonnes ha^{-1} (Table 2). The range in CWD across the sampling grid was large (0–154.5 tonnes ha^{-1}). As indicated by the small median (1.4 tonnes ha^{-1}), the frequency distribution of CWD was strongly right skewed. Six plots (7.4%) had loads more than three times the mean CWD, four plots (4.9%) were more than six times the mean. Less than average values for density (Fig. 3), percent cover, volume (Fig. 4), and weight were recorded in 57%, 64%, 67%, and 69% of the plots, respectively.

All of the CWD were in the later stages of decay; none of the samples were identified as decay class 1 (Table 3). Large end diameter of CWD ranged from 15 to 96 cm. Most of the hard CWD (decay classes 1–3) had average diameters less than 45 cm (Table 4). The majority of logs inventoried (56.9%) were rotten (decay classes 4–5, Table 5). Most of the CWD was Jeffrey pine (73.5%), with white fir contributing a relatively small amount (12.8%); 13.7% of the CWD could not be identified to species (Table 6).

It was not possible to crossdate any of the CWD wedge samples to determine the year that an individual tree died. Most samples were excessively rotten and this prevented accurate

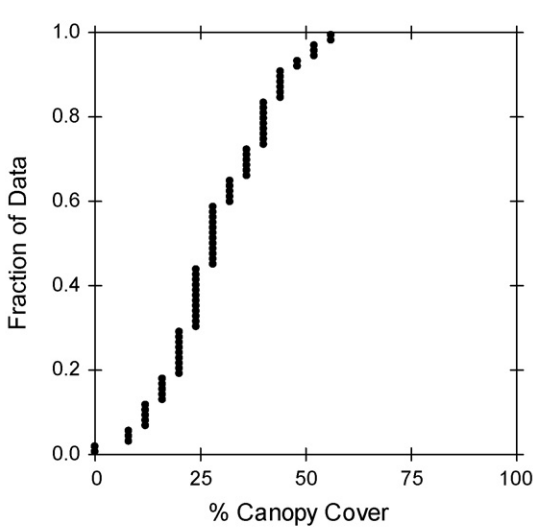

Fig. 2. Quantile plot of canopy cover using a sight tube in Jeffrey pine-mixed conifer forests in the SSPM, Mexico ($n = 121$).

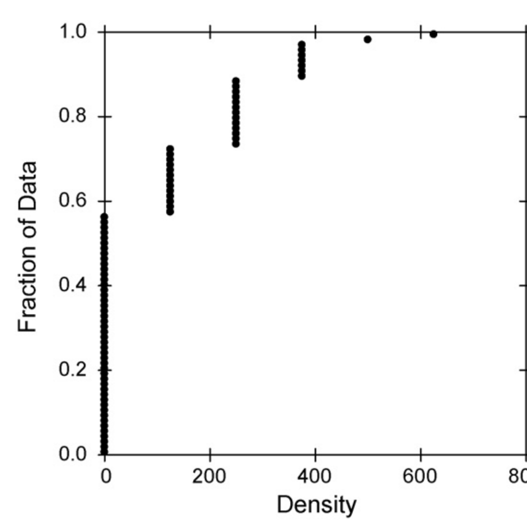

Fig. 3. Quantile plot of CWD density (pieces ha^{-1}) in Jeffrey pine-mixed conifer forests in the SSPM, Mexico ($n = 81$).

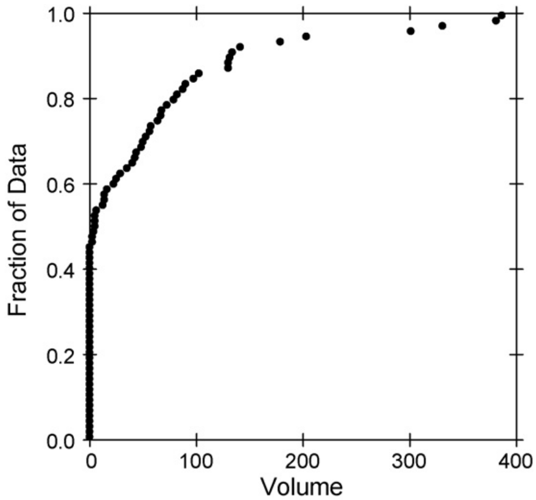

Fig. 4. Quantile plot of CWD volume ($m^3\ ha^{-1}$) in Jeffrey pine-mixed conifer forests in the SSPM, Mexico ($n = 81$).

crossdating. A few wedge samples included tree-ring series that could be crossdated to the nearby chronology (Stokes et al., 1971) but the outer most ring was not intact in any of the collected samples.

4. Discussion

CWD dynamics in forests that experience frequent, low-moderate intensity fires are fundamentally different than those having long-interval, high-severity fires. Persistent, recurring fires (fire return intervals <30 years) in concert with other disturbances (wind, insects, disease, drought) would both destroy and create CWD throughout forest development. Since many of these forests did not commonly experience stand-replacement fire in areas larger than a hectare (Moore et al., 1993; Biondi, 1998; Fulé et al., 2002; Stephens and Fry, 2005), large-scale episodic CWD recruitment would not be an important process. Rather, small-scale disturbances (fire, insects, diseases, drought, wind, combination of these factors) could kill an individual tree or a small group of trees, resulting in recruitment of new CWD; the same fire that killed trees would also consume existing CWD.

The distribution of CWD in the SSPM was patchy with approximately 50% our sampled plots having no CWD and 12.3% of the plots containing three to six times the mean CWD load. In addition, rotten CWD was more abundant than sound CWD in the forests of the SSPM. This suggests that CWD created by small-scale disturbances can exist in some locations

Table 3
Average (S.E.) CWD characteristics by decay class in Jeffrey pine-mixed conifer forests in the SSPM ($n = 81$)

Decay class	n (pieces)	Diameter (cm)	Density (pieces ha^{-1})	% Cover (ha^{-1})	Volume ($m^3\ ha^{-1}$)	Weight (tonnes ha^{-1})
1	0	–	–	–	–	–
2	2	28.0 (0.6)	3.1 (2.2)	0.0 (–)	0.6 (0.5)	0.3 (0.2)
3	42	27.5 (1.5)	44.8 (12.1)	0.5 (0.1)	13.9 (5.4)	5.6 (2.2)
4	37	36.4 (2.0)	35.5 (8.3)	0.6 (0.2)	21.7 (6.7)	6.6 (2.0)
5	21	40.7 (1.8)	24.7 (7.7)	0.3 (0.1)	11.0 (3.1)	3.3 (0.9)

S.E. is the standard error of the mean.

Table 4
Average (S.E.) CWD characteristics by diameter class (decay classes 1–3) in Jeffrey pine-mixed conifer forests in the SSPM ($n = 81$)

Diameter class (cm)	n (pieces)	Diameter (cm)	Density (pieces ha^{-1})	% Cover (ha^{-1})	Volume ($m^3\ ha^{-1}$)	Weight (tonnes ha^{-1})
15–30	29	20.9 (0.6)	37.0 (7.6)	0.2 (0.0)	2.9 (0.6)	1.2 (0.3)
30–45	12	34.3 (0.9)	10.8 (4.1)	0.2 (0.1)	5.5 (2.0)	2.2 (0.8)
45–60	1	45 (–)	0 (–)	0 (–)	0.4 (–)	0.2 (–)
60–75	1	70 (–)	0 (–)	0 (–)	1.1 (–)	0.4 (–)
75–90	1	80 (–)	0 (–)	0.1 (–)	4.6 (–)	1.8 (–)
90–105	0	–	–	–	–	–
All classes	44	27.6 (1.9)	47.8 (8.7)	0.5 (0.1)	14.5 (5.2)	5.8 (2.1)

S.E. is the standard error of the mean.

Table 5
Average (S.E.) CWD characteristics by diameter class (decay classes 4–5) in Jeffrey pine-mixed conifer forests in the SSPM ($n = 81$)

Diameter class (cm)	n (pieces)	Diameter (cm)	Density (pieces ha^{-1})	% Cover (ha^{-1})	Volume ($m^3\ ha^{-1}$)	Weight (tonnes ha^{-1})
15–30	20	20.1 (1.0)	26.2 (6.4)	0.1 (0.0)	1.8 (0.5)	0.5 (0.2)
30–45	21	37.6 (1.1)	20.1 (5.6)	0.3 (0.1)	8.9 (2.2)	2.7 (0.7)
45–60	9	50.4 (1.1)	10.8 (4.1)	0.2 (0.1)	6.7 (2.6)	2.0 (0.8)
60–75	7	65.9 (1.3)	3.1 (2.2)	0.3 (0.1)	11.5 (4.6)	3.5 (1.4)
75–90	0	–	–	–	–	–
90–105	1	96 (–)	0 (–)	0.1 (–)	4.0 (–)	1.2 (–)
All classes	58	38.0 (2.3)	60.2 (9.7)	0.9 (0.2)	32.9 (7.0)	9.9 (2.1)

S.E. is the standard error of the mean.

Table 6
Average (S.E.) CWD characteristics by species in Jeffrey pine-mixed conifer forests in the SSPM ($n = 81$)

	Jeffrey pine	White fir	Unknown
n (pieces)	75	13	14
Diameter (cm)	34.4 (2.0)	36.9 (4.2)	25.1 (3.5)
Decay Class	3.6 (0.4)	4.1 (0.2)	4.1 (0.2)
Density (pieces ha^{-1})	71.0 (10.5)	17.0 (5.2)	20.1 (5.6)
Cover (% ha^{-1})	1.2 (0.2)	0.2 (0.1)	0.1 (0.1)
Volume (m^3 ha^{-1})	38.8 (8.3)	5.5 (2.2)	3.1 (1.4)
Weight (tonnes ha^{-1})	13.0 (2.9)	1.7 (0.7)	1.0 (0.4)

S.E. is the standard error of the mean.

for relatively long periods of time within a highly fire prone ecosystem. Rotten CWD would be highly susceptible to ignition by burning embers or direct flame contact.

Stephens and Moghaddas (2005) documented a reduction of 76–99% of rotten CWD after one prescribed fire in mixed-conifer forests in the north-central Sierra Nevada. This area had not been burned for approximately 90 years (Stephens and Collins, 2004) and it had high horizontal fuel continuity. The high horizontal fuel continuity resulted in a high percentage of area burned within the prescribed fire units. Jeffrey pine-mixed conifer forests in the SSPM have low horizontal fuel continuity (Stephens, 2004) and this would result in a lower percentage of the landscape burning during each fire. Low horizontal fuel continuity probably allows some CWD to remain in the forest after repeated fires.

With respect to potential standing woody debris pools in the form of snags, Holden et al. (2006) found significant reductions in densities of large (>47.5 cm DBH) snags between areas burned once, though no significant differences in large standing snag densities between areas burned under wildland-fire-use two or three times. Based on the findings from this study and Holden et al. (2006), it appears that sound and rotten CWD can remain on particular microsites that do not burn as often when subjected to the same fire regime. Under these conditions, fire would have burned multiple times within the vicinity of the rotten and sound CWD measured in this study. The lack of fire in microsites where CWD was clustered may be due to topography, rocky substrates, or some other barrier to surface fire spread and spot fire embers, or it may simply be the laws of chance where some areas will simply be unburned. Livestock grazing in the forested areas of the SSPM has not reduced grass fuels (Evett et al., in press) and probably has not impacted the regions fire regime.

CWD density, percent cover, volume, and weight are larger in xeric Jeffrey pine-mixed conifer forests in the SSPM when compared to xeric ponderosa pine (*Pinus ponderosa* Laws.) forests in Colorado and in eastern Washington and Oregon (Table 7). One probable cause for these differences is past harvesting which has occurred in most of these ponderosa pine forests. The majority of past harvests in the western US have targeted large, mature trees because they had the greatest economic values; large trees were also sometimes removed to open up resources (light, water, etc.) to increase the growth rates of smaller trees. In either circumstance, the removal of these large, mostly older trees would decrease the pool for future CWD recruitment, especially in the larger size categories. In contrast to most western US forests, few trees have left their stumps in the SSPM (the exception being some light harvesting that affected only a few hectares of forests well away from our study site). Since no trees have been removed from our study area, it is logical to expect these forests to have higher amounts of larger CWD when compared to harvested, xeric pine-dominated forests that once experienced frequent, low-moderate intensity fire regimes. Though there are no ponderosa pines in the SSPM, the relationship of Jeffrey pine to fire is usually considered similar to ponderosa pine (Habeck, 1992). However, there appears to be more variability in Jeffrey pine fire regimes in regions where the two species overlap (Skinner and Chang, 1996).

In the more productive mixed-conifer forests of the northern Sierra Nevada, not only is there is there more CWD (abundance and volume), CWD is dominated by sound materials (Sierra Nevada mixed-conifer forest, sound CWD density 167 pieces ha^{-1}, volume 58 m^3 ha^{-1}, rotten CWD density 87 pieces ha^{-1}, volume 39 m^3 ha^{-1}; SSPM Jeffrey pine-mixed conifer forest, sound CWD density 48 pieces ha^{-1}, volume 14 m^3 ha^{-1}, rotten CWD density 60 pieces ha^{-1}, volume 33 m^3 ha^{-1}) (Stephens and Moghaddas, 2005). Mixed-conifer forests in the northern Sierra Nevada have experienced a much different management history when compared to forests in the SSPM. Much of the Sierran mixed-conifer forests were heavily

Table 7
Comparison of average CWD characteristics in coniferous forests in the western US and the Sierra San Pedro Martir, Mexico

Source	Location	Forest type	Density (pieces ha^{-1})	Volume (m^3 ha^{-1})	Cover (% ha^{-1})	Weight (tonnes ha^{-1})
Ohmann and Waddell (2002)	East of the Cascade crest in Oregon and Washington	Eastside ponderosa pine	74	25	0.9	–
Robertson and Bower (1999)	Front Range Colorado	Ponderosa pine	–	12	–	3
Robertson and Bower (1999)	Southwestern Colorado	Ponderosa pine	–	23	–	5
Knapp et al. (2005)	Sequoia National Forest, southern Sierra Nevada	Upper mixed conifer	173	190	4.3	62
Stephens and Moghaddas (2005)	Blodgett Forest Research Station, north-central Sierra Nevada	Mixed conifer	187–254	51–53	2–2.3	35
This work	Sierra San Pedro Martir National Park, Northern Baja California	Jeffrey pine-mixed conifer	108	48	1.5	16

harvested in the early 1900s using railroad logging systems (Stephens and Collins, 2004). Continued harvesting in the forests of the northern Sierra Nevada for the last 50–100 years would have reduced the large CWD pool.

The northern Sierra mixed-conifer forests regenerated naturally following harvesting in the early 1900s and many are at a stage of stand development where mortality is occurring because of limited resources (e.g. stem exclusion phase). This mortality, combined with the complete absence of fire because of fire exclusion, and higher site productivity, leads to the greater amounts of CWD in the Sierra Nevada forests (Knapp et al., 2005). However, CWD in Sierran mixed-conifer forests that have been repeatedly harvested is composed of relatively small CWD due the removal of most large trees and to the input of un-merchantable material (e.g. tree tops and large limbs) from harvesting operations.

Ohmann and Waddell (2002) report that in eastside ponderosa pine forests in Washington and Oregon, large CWD was not abundant outside wilderness areas. They further report that US Occupational Health and Safety Administration (OSHA) standards require the felling of most snags from harvest units for forestry worker safety. Many eastside forests in Washington and Oregon currently have elevated surface fuel loads due to fire suppression (Ohmann and Waddell, 2002). The need to reduce surface fuel loads, including CWD in the smaller size classes, while at the same time recruit large CWD presents a real dilemma for managers.

Jeffrey pine forest canopy cover data are limited but one study in this forest type in the eastern Sierra Nevada, canopy cover and canopy closure were 27.8 and 44.4%, respectively (Stephens, 2001). Average canopy cover and closure in Jeffrey pine-mixed conifer forests in the SSPM is 26.8 and 40.1% using the sight tube and spherical densiometer, respectively. Forest canopy cover is very similar even though the eastern Sierra Nevada site has been subjected to fire suppression for 90 years. Canopy cover would increase slowly in relatively dry, unproductive, pine-dominated forests and this probably explains why the differences between the two sites are small.

It is important to specify the type of instrument used to measure forest canopies because each instrument quantifies different characteristics; canopy cover is the porosity of the canopy at the stand level while canopy closure is foliage cover over one point. The ecological relevance of each (cover being important to stand-level microclimate and prey protection while closure directly influences understory light and temperature at a given point) measurement is needed to interpret their biological importance.

It is common for US fire hazard assessment systems to assume that forests which have missed more fire-return intervals will have higher hazards (Schmidt et al., 2002). Although many ponderosa and Jeffrey pine forests have missed 10 fire intervals, the effects of 90 years of fire suppression on the amount of canopy cover and CWD may be greater in a more mesic mixed-conifer forest, which have only missed 3–4 fire intervals (Franklin and Agee, 2003; Stephens, 2004; Stephens and Ruth, 2005). This occurs because mixed-conifer forests are generally more productive resulting in more rapid structural change.

5. Conclusions

There was a large amount of variability in all CWD and forest canopy cover measurements taken from old-growth Jeffrey pine-mixed conifer forests in the SSPM. Even though average CWD load was 15.7 tonnes ha^{-1}, the range of values was 0–154.5 tonnes ha^{-1} and close to half (45.7%) of all plots measured had no CWD present. Six plots had more than three times the mean CWD load, four plots were more than six times the mean load. Forest canopy cover in the SSPM was also quite variable (Fig. 2).

This work and another study published from the SSPM on fuels and snag characteristics (Stephens, 2004) clearly demonstrate that managing for average structural characteristics on every ha at the stand scale (10–25 ha) replicated many times over landscapes scales is not appropriate if your objective it to produce a resistant ecosystem. It may be more appropriate for managers to create a range of desired conditions rather than managing for average conditions in each stand.

The SSPM has a high amount of spatial heterogeneity in forest structure and this property probably reduced forest mortality when it was subjected to severe drought from 1998 to 2002 (Stephens, 2004). Similar forests in the northern Peninsular Range in southern California (these forests have much higher stand densities and lower spatial heterogeneity because of fire suppression and past harvesting) experienced a similar drought but tree mortality there was one to two orders of magnitude larger (Stephens and Fulé, 2005). Spatial heterogeneity in forest structure should be included in the desired conditions of xeric, pine-dominated forests in the US that once experienced frequent, low-moderate intensity fire regimes. It should be noted that heterogeneity by itself may not lead to sustainable forests unless that heterogeneity includes stand structures that are resistant/resilient to high-severity fire, drought, insects and disease.

Acknowledgments

This project was supported by University of California Agricultural Experiment Station research funds. We appreciate the assistance provided by Travis Freed, Dan Stark and Brett Goforth. The research reported here was carried out under permits (NUM/SGPA/DGVS/3315; UM/SGPA/DGVS/04036; 10 NUM/SGPA/DGVS/04075) issued by the Mexican Ministry of the Environment (SEMARNAT) for the project, “Cronologia de incendios y cambios climaticos y de vegetacion en los bosques de coniferas mixtas de la Sierra de San Pedro Martir, Baja California, México.”

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